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AN IMPROVED, CONCEPTUALLY SIMPLE TECHNIQUE FOR ESTIMATING THE PRODUCTIVITY OF MARSH VASCULAR FLORA

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ABSTRACT The estimation of the net primary productivity of marsh communities with a periodic maximum–minimum (PMM) technique has certain advantages over the long used maximum–minimum standing stock technique, but still retains the same conceptual simplicity. The final productivity estimate with PMM is based on the entire data set rather than just two points. Direct statistical comparisons between any two communities can be made. An estimate of the productivity by minor species in the community can also be made. The periodic model permits statistical comparisons about other variables in community growth such as the timing of the maximum standing crop. With certain assumptions, productivity estimates which account for the loss of live plant material during the growing season can be made without the tremendous amount of effort and time required by the Wiegert–Evans technique. Despite the increased utility the PMM technique requires no additional field effort.

INTRODUCTION

The productivity of coastal tidal marshes is a useful way to compare the potential productivity of estuaries (Turner 1977). Estimation techniques for tidal marsh productivity range from conceptually simple techniques such as the standard maximum–minimum (max–min) standing crop technique to techniques that measure the disappearance of material from plots in addition to the increase in living plant material (Wiegert and Evans 1964). Each technique has certain advantages over other techniques. The Wiegert–Evans technique may provide a better estimate of plant productivity, but requires more time and effort than the standard max–min technique. Determination of the best technique depends greatly on the amount of effort available, the community to be studied, and the eventual use of the data. The ideal technique must account for (1) the variation of plant density throughout the study marsh;(2) the inherent variation between sampling dates;(3) the death of new plant growth during the growing season; (4) the productivity of minor plant species in the community; and (5) loss of new plant growth through herbivory.

The following is a method for estimating marsh plant productivity using the conceptual simplicity of the max–min technique, but allows the researcher to account for these other variables in his estimate. The use of a statistical model improves the reliability of the productivity estimate and provides a valid mathematical model through which other tests and comprisons can be made. These advantages are added without substantially increasing the amount of effort required for the max–min technique. The technique also has the advantage of allowing straight-forward statistical comparisons between any two studies regardless of when or where they are made. The periodic model has widespread application and has provided a good fit for many other biological phenomena (Odum and Smalley 1959; Buzas 1969; Brown and Taylor 1971; Hackney et al. 1976).

METHOD

The periodic regression model differs from the usual general regression model only in the functional form of the independent variable. The usual general one-term linear regression model is:

$$y_i = \alpha + \beta x_i + e_i \qquad i = 1, \ldots, n.$$

The corresponding one-term periodic model considers the trigonometric functions of x_i as

$$y_i = \alpha_0 + \alpha_1 \cos(cx_i) + \beta_1 \sin(cx_i) + e_i \qquad (1)$$

where

y_i = dependent variable
α_0 = constant parameter
α_1, β_1 = coefficients of the harmonic function of x_i
c = $2\pi/n$
x_i = i th independent variable
e_i = error.

Note that a pair of trigonometric terms constitute a single harmonic term. In most ecological problems the independent variable x_i is time, each x_i representing a unit of time such as months, $i = 1, 2, \ldots, 12$. The dependent variable y_i could be temperature, salinity, number of organisms, etc.

The semi-amplitude of the curve described in equation (1) would be

$$A = \hat{\alpha}_1^2 + \hat{\beta}_1^2$$

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and the phase angle estimated by

$$\operatorname{Tan}(\hat{\theta}) = |\hat{\beta}_1 / \hat{\alpha}_1| \ .$$

The number of terms in the model is determined in the same manner as choosing the number of terms in any regression model. The goal is to find a model that adequately describes the data, and also has biological validity. As in polynomial regression, it is possible to add enough terms to the periodic model to achieve an exact fit. The addition of harmonic terms should depend upon the biological interpretation of the model. If only the diel cycle is known to effect a given phenomenon yet five harmonics are required to explain the data, then the model is probably incorrect. Other factors, not necessarily periodic, might need to be considered in the model. The periodic model usually provides an excellent fit for productivity data (Bliss 1970; Hackney and Hackney 1977). This technique allows the use of stratified sampling collection procedures which are less destructive to marshes than simple random collection techniques and less time consuming. Since the fitted curve used samples collected over the entire marsh, the final resulting max–min values reflect the variation in plant density within the marsh as well as the inherent error between samples. The standard max–min procedure only reflects the variation of the highest and lowest biomass estimates. Estimation of the productivity of minor species can be made using the same periodic curve with these same conceptual advantages overcoming the usual patchiness of minor plant species distribution, essentially integrating this highly variable component into a smooth curve. If data are available on the death rate of plants within the community, a productivity estimate may be obtained that, like the Wiegert–Evans technique, includes productivity lost by the early death of plants. In many cases these data are available with little increase in effort.

Examples

The data used in the following examples were collected in a Mississippi tidal marsh located on the western side of St. Louis Bay, Mississippi. The vegetation on this marsh was described by Gabriel and de la Cruz (1974).

The increase of above-ground vascular plant biomass in marshes usually follows a periodic type of curve as does the increase in the below-ground portions of these plants (de la Cruz and Hackney 1977). An examination of the means of each collection plotted against time will provide visual proof of whether the periodic model is appropriate. In the following examples five 0.25 m^2 samples were collected on each date. The first example demonstrates what factors are used to determine the validity of the model and the difference between a productivity estimate made through the periodic max–min technique and an estimate with the standard max–min technique. The second example provides a mathematically sound method of estimating the contribution by minor plant species in the community, while the third example compares two models that produced similar quantities of biomass, but produced them at different times. The last example shows how a better productivity estimate can be obtained if information on the death rate of the plants is known.

One disadvantage of the traditional max–min technique is that it uses only two values from the entire year's collection, the highest and lowest standing crop of living plant material. With this technique the community in Figure 1 had a productivity of 481 $g/m^2/yr$. A periodic curve fitted to all of the data points also provides a maximum and minimum value, but these values are based on the entire data set and the variability of all samples. There were 372 $g/m^2/yr$ of vascular plant production estimated by this technique. The periodic model of the *Juncus* community in Figure 1 is

$$Y = 770.9 - 88.7 \sin(ct_i) - 162.9 \cos(ct_i)$$

where $c = 2\pi/12$ and $t_i = 1, \ldots, 12$ based on 40 observations. The r^2 was 0.493 with a significant F of 18.0 which indicates a significant ($\alpha = 0.05$) periodic component and a significant r^2 in the data set. The test of a significant periodic component is the most important factor when deciding whether to accept the use of the periodic model. If this component were nonsignificant a model based just on the overall mean would be more appropriate. More information on the actual testing of periodic models is provided by Hackney and Hackney (1977). The variability of plant distribution within a marsh plant community may cause what seems to be low r^2 values. This variability affects the r^2 most if a random stratified sampling scheme is used. If one is willing to accept the assumption that the

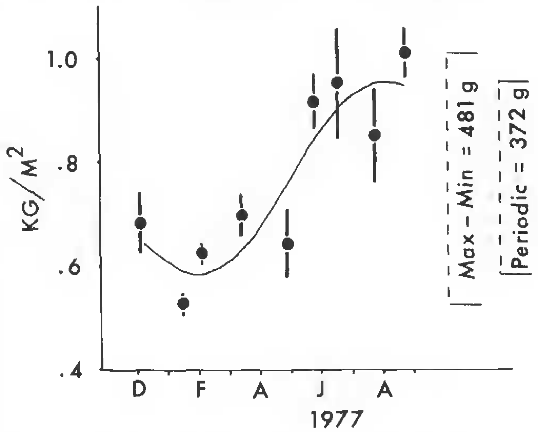

Figure 1. Monthly changes of live biomass in a *Juncus* community. Vertical lines represent ± one standard error. The smooth curve is predicted from the periodic model. Estimates derived by the simple max–min technique and the periodic model are compared.

increase in plant biomass follows a periodic pattern then a random stratified sampling procedure may be used, which does not disturb the marsh, and is not as time consuming as the simple random collection technique.

Perhaps the most difficult component to isolate in a marsh plant community is the contribution of the minor species to the productivity of the community. This may be done through the development of a periodic model for the increase of living plant biomass for the entire community, and a separate model for the dominant plant species, in this example *Juncus roemerianus* (Figure 2). Subtraction of the two productivity estimates yields an estimate of the contribution by the minor plant species in the community, which in this case was 56 g/m^2/yr.

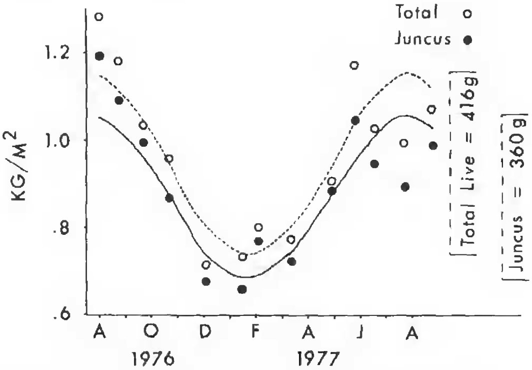

Figure 2. Periodic models of the total live plant biomass and the total live *Juncus* in a control community. The mean of each monthly collection is provided for comparison. The difference between the productivity estimates is an estimate of the productivity of the minor species in the community.

Another useful aspect of this technique is the ability to test whether the growth (productivity) of two communities is the same. Using the standard max–min technique one has two numbers to compare and no way to make a statement about any statistically significant differences between the two communities. In the following example, two *Spartina cynosuroides* communities were compared the second year following a burn in one community (Figure 3). A comparison of the two periodic models indicated that there was no significant difference ($\alpha = 0.05$) in the amount of live biomass produced, but that the peak production was reached earlier in the burned community. This type of information is not available directly from other estimation techniques. Interpretation of the analysis of variance (ANOVA) output necessary to make these decisions is provided by Hackney and Hackney (1977).

Despite the reliability realized through the use of this periodic max–min technique there are still certain components of plant productivity that are not considered. Hopkinson et al. (in press) emphasized the need for any

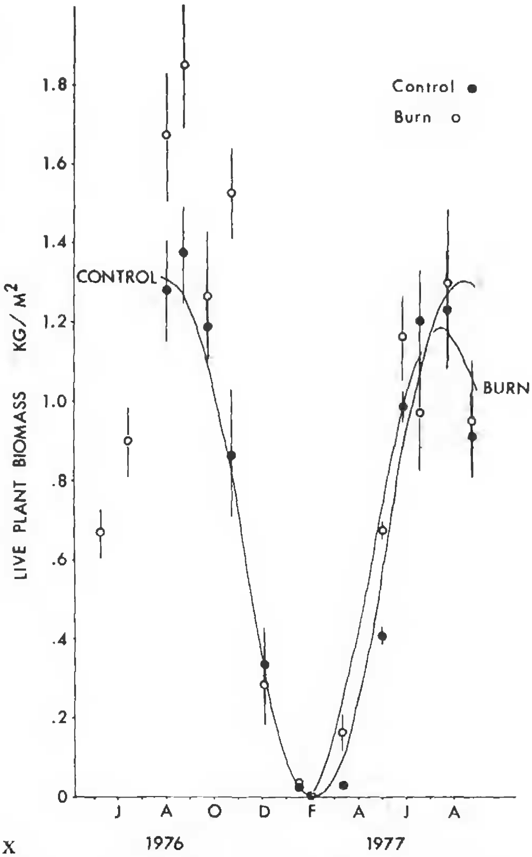

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Figure 3. Periodic models of the natural and burned *Spartina cynosuroides* community. Individual points represent the mean ± one standard error.

productivity estimate to account for the loss of dead plant material from a community. This is most important if the above-ground portions of the plant do not die during the winter, such as *J. roemerianus* along the Gulf coast or if the turnover rate is very high. To integrate this component into a periodic max–min estimate one can produce a mathematical model based on the accumulation of dead material during the growing season. It is necessary to be sure that this dead material was produced during the growing season. To do this an area can be cut at the beginning of the growing season and samples collected from this area each month. In the case of plants that die each winter, cutting does not seem to affect the accumulation of dead material during the growing season. The only potential effect is the lack of shading that may be produced by the previous year's dead standing biomass. In the case of perennial plants (*Juncus*, etc.) which stay green all year this practice may have some effect. The addition of this component to the productivity estimate may require the addition of a significant amount of field work to the study. In the following example this was not a factor since the intent was to estimate the productivity of a *Juncus* community following a fire. A general model that combined a periodic component with an asymptotic exponential function provided a good fit for the increase of dead material in the burned *Juncus* community. Models besides the asymptotic exponential would be adequate provided that they adequately represent the data. The predicted model of the live biomass, dead biomass and the combined model (Figure 4) illustrates the need to account for this dead component. In this particular case 115 g/m^2 was added to the annual productivity of this community by accounting for the loss of new living material during the growing season.

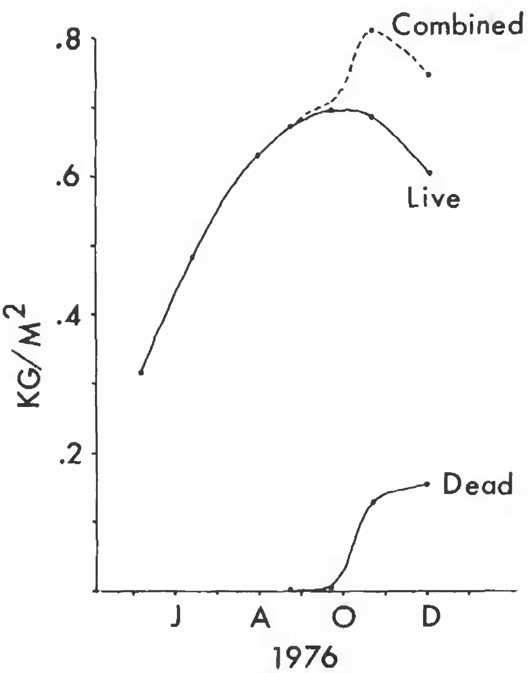

Figure 4. Periodic model of the living plant biomass, model of the accumulation of dead plant material and the combined value of a burned *Juncus* community.

DISCUSSION

The measurement of net primary productivity in any marsh system is necessary to completely understand the energetics of that system. Techniques that measure other factors besides changes of live biomass (Wiegert and Evans 1964) may be useful if the additional time and effort are available. It is unlikely that the literature on marsh plant productivity will ever achieve the uniformity that Turner (1976) and Kirby and Gosselink (1976) feel is necessary when other researchers consider the max–min technique adequate (de la Cruz 1978). The periodic max–min technique (PMM) could provide uniform estimates of marsh plant productivity since most of the published data could easily be recalculated using this technique. The technique still possesses the conceptual simplicity which de la Cruz (1978) believed desirable. With only a small amount of increased effort other factors such as the instantaneous loss rate, productivity of minor species in the community, and various sampling problems can be accommodated with the PMM technique. Kirby and Gosselink (1976) fitted a polynomial function to the changes of live and dead material they found in a salt marsh. These data could have been easily fitted to a periodic model. The biological interpretation of a polynomial model is not usually apparent, while the interpretation of a periodic model is usually straight forward. For example, a fourth-degree polynomial is equivalent to a single harmonic model. Interpreting the meaning of raising an independent variable, e.g., time, to the fourth power is more difficult than explaining a single cycle over a specified interval. Also direct estimates of amplitude and phase are available. Periodic models may also reveal differences between communities via periodic regression analysis (Hackney and Hackney 1977).

The calculation of the actual primary productivity of marsh plants is difficult. In the past we have separated the productivity of the aerial portion of the plant (leaves and stems) from the productivity of the roots and rhizomes. This below-ground productivity may be as high as the above-ground productivity (de la Cruz and Hackney 1977). More recently Hopkinson et al. (in press) have shown that productivity estimates that do not consider the short-term turnover rate may greatly underestimate the primary productivity of some marsh plant species. The estimation of the loss of newly produced plant material (instantaneous loss rate) in a marsh community has many associated problems (Hopkinson et al., in press). A relatively simple method of estimating this loss rate is shown in Figure 4. This technique would not be appropriate for plants with a rapid turnover rate and would not be as good an estimate as that obtained by the paired plot technique of Hopkinson et al. (in press). Both techniques require the disturbance of an area by the researcher that could affect the final results. The effect of clipping all vegetation from an area and then following the accumulation of dead material during the growing season may not affect the resultant estimate any more than the variables introduced by the Wiegert–Evans technique.

Hopkinson et al. (in press) suggested that the max–min technique underestimated the actual productivity of marshes because it does not account for the loss of newly produced organic matter. An additional criticism of the standard max–min technique is that it provides a poor estimate of the actual increase of living plant biomass because it is based on only two points, each of which is subject to the inherent variability found in any natural system (Figure 1). The periodic max–min technique provides an estimate that is based on every sample collected during the study. Thus, the primary productivity estimate obtained through the periodic max–min technique may be higher or lower than the standard max–min technique, but is far more reliable. If the model which predicts the loss of new plant growth is added to the periodic model, an estimate is produced that is higher than either of the max–min estimates and comparable to the Wiegert–Evans technique.

Since the periodic max–min technique is easy to use, conceptually simple, and satisfies some of the criticisms of other techniques, it is suggested as the best general method available to estimate the net primary productivity in marsh communities.

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